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factors, we then naturally wonder just what part "distance between two genes" on a chromosome map may play in determining linkage values. Our current view is that "the percentage of cases in which two linked genes separate (amount of crossing over between them) is necessarily proportional to the distance between these genes,—other things being equal," i. e., under ordinary circumstances and in the absence of unusual factors or environmental conditions which geneticists recognize. But evidently under ordinary circumstances, the percentage of crossing over is a variable which is determined by the different possible combinations of multiple modifying factors; hence the percentage of crossing over cannot be proportional to the distance if the distance remain constant. For example in Series *B* we find 6% crossing over, and so we should conclude that the distance is less than one-fifth of what it originally was before we began selection. To maintain our original position, we must conclude that the percentage of crossing over and the distance are correlated variables, if the proportion is to remain reasonably constant. The dilemma will hardly aid us in determining what had happened to almost all of the distance and the genes between 0 and 33 in Series *A* and *A'*, where crossing over was practically eliminated. In view of these considerations it would perhaps be simpler to conclude that linkage is not a function of distance, i. e., crossing over is not necessarily proportional to distance. The distance between two genes may remain fairly constant, but the amount of crossing over depends upon numerous hereditary factors.

<sup>1</sup> Paper No. 14 from the Laboratory of Genetics, Illinois Agricultural Experiment Station.

<sup>2</sup> In giving crossover values, I shall put the data in the following form throughout this paper—crossovers: total = per cent of crossing over. Since the classes are always the same, repetition can be avoided.

<sup>3</sup> I am indebted to Dr. E. Roberts and Mr. P. M. Woodworth for carrying this generation in part.

## INTERSPECIFIC HYBRIDS IN CREPIS

### I. *Crepis capillaris* (L.) Wallr. $\times$ *C. tectorum* L.

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Interspecific hybrids, particularly those having different specific chromosome numbers, have in the past figured conspicuously in establishing the now generally accepted principle of the individuality and continuity of the chromosomes. It is probable, therefore, that a study of the hereditary characters of species hybrids may give further information concerning the chromosomes as the carriers of the determiners of hereditary characters

and add to our knowledge regarding the manner of the origin and evolution of specific chromosome numbers.

From a study of interspecific crosses between *Nicotiana sylvestris* and several varieties of *Nicotiana Tabacum*, Clausen and Goodspeed<sup>1</sup> have found that the Mendelian laws apply but apparently the chromosomes of the hybrid will function normally only when there is a union of a majority of the chromosomes of one species. When the chromosomes of one gamete are mostly of a different species from those of the other uniting gamete the zygote either does not live or it develops abnormally. This seems to indicate that although they are numerically the same, the chromosomes of the two species differ so much qualitatively that they cannot properly function together.

Eggs of the sea urchin have been fertilized artificially with the sperm of another species in which the chromosomes were different in number. In practically all such cases the zygote would start but fail to complete development. It appears that the chromosome complex sets up an incompatible combination of genes such that the embryo cannot pass a certain stage of differentiation.

The writers have found a somewhat similar case in plants in the hybrid between *Crepis capillaris* and *C. tectorum*. This genus belongs to that tribe of the Compositae having the heads composed entirely of ligulate flowers. *C. tectorum* is an annual and *C. capillaris* behaves either as an annual or as a biennial. The former has four pairs of chromosomes while the latter, *C. capillaris*, has but three pairs. Cytological studies have shown the hybrid to have seven chromosomes, the sum of the haploid numbers of the two species.

The differences between the two species are quite marked. The achenes of *tectorum* are about 4 mm. long, are dark brown in color and retain the pappus quite well. The cotyledons are narrowly linear with obtuse apex, the shape resembling that of a sunflower seed or the cotyledons of a very young cucumber seedling. The first plumule leaf appears very promptly soon after the cotyledons have expanded and reached their maximum size. The plants often reach maturity in ninety days. The achenes of *capillaris* are about 2.5 mm. long, are tan or straw color, and shed the pappus rather easily. The cotyledons vary from broadly ovate to the condition where the breadth is slightly greater than the length. As in *tectorum* the first plumule leaf appears very promptly after the cotyledons have expanded to their normal size.

In the hybrid, regardless of the way the cross is made, we find that the *tectorum* type of cotyledon is dominant but the seedlings are larger than the normal *tectorum* seedlings and may in that respect be said to show hybrid vigor. That the shape and size of the hybrid cotyledons growing on a *tectorum* mother plant would be comparable to the cotyledons

from a pure *tectorum* achene of the same size would not be surprising but that the cotyledons coming from the much smaller *capillaris* achenes should be so much larger than those usually coming from ordinary *capillaris* achenes seems unusual and gives immediate evidence of the hybrid nature of the seedling.

The hybrid seedlings grew very vigorously through the cotyledon stage, then growth and development ceased although different plants remained alive from 30 to 81 days in this arrested condition. All hybrids died before passing beyond this stage of development. The attempt to grow the hybrid between these two species was made three separate times always with the same behavior and the same results.

TABULATION OF RESULTS OF RECIPROCAL CROSSES

CULTURE NO.	PARENTS	COTYLEDON CHARACTERS OF HYBRID	BEHAVIOR OF HYBRID	NUMBER OF SEEDLINGS
Z 3	<i>capillaris</i> × <i>tectorum</i>	6 <i>tectorum</i> , 5 <i>capillaris</i> , 1 intermediate	all failed to pass cotyledon stage	12
Z 5	<i>capillaris</i> × <i>tectorum</i>	all <i>tectorum</i> ; showed hybrid vigor	all failed to pass cotyledon stage	6
Z 7	<i>capillaris</i> × <i>tectorum</i>	all <i>tectorum</i> ; showed hybrid vigor	all failed to pass cotyledon stage	3
Z 8	<i>capillaris</i> × <i>tectorum</i>	intermediate	failed to pass cotyledon stage	1
Z 10	<i>tectorum</i> × <i>capillaris</i>	all <i>tectorum</i> ; showed hybrid vigor	all failed to pass cotyledon stage	12
Z 12	<i>capillaris</i> × <i>tectorum</i>	small and distorted, abnormal	failed to pass cotyledon stage	1
Z 13	<i>capillaris</i> × <i>tectorum</i>	small and distorted, abnormal	all failed to pass cotyledon stage	5

Histological examination of a hybrid seedling revealed a most unusual teratological condition of the tissue systems and of the cells which, no doubt, was the immediate cause of the unusual behavior noted. These tissue systems were in a chaotic condition where order and continuity should be expected. Patches of embryonic tissue were scattered irregularly among the vegetative cells, patches of tracheary cells were likewise found here and there in the meristematic tissue of the seedling. In fact, tracheary cells were in one section found to be extending at right angles to the long axis of the seedling. Groups of vegetative cells were separated by streaks of disorganized and disintegrating tissue. Some of the vegetative cells were abnormally large.

In this interspecific hybrid it appears as if the force directing cell differ-

entiation were lacking or non-functioning. We know that in all promeristematic cells there must be the potentiality for development of a complete individual but that during development something determines what, when and where tissues and organs shall be developed. In these hybrids that force is not acting, in a normal way at least, and hence the cells develop the various tissues in a haphazard way and otherwise misbehave.

The opinion has been expressed a number of times that the different species of a single genus having different chromosome numbers may have been derived, the larger from the smaller number, by fragmentation or by duplication resulting from non-disjunction during synopsis. Rosenberg<sup>2</sup> has recently worked out the specific chromosome number of 15 species of *Crepis* (published 19, 4 having been determined by other cytologists). He expressed the belief that the species having four and five pairs of chromosomes could have been formed by non-disjunction occurring during the reduction division. Bridges<sup>3</sup> has shown that such behavior is possible, at least for the sex chromosomes in *Drosophila*, for he has found flies with ten chromosomes, the typical number for the species being eight. The increased number came about through secondary non-disjunction of the sex chromosomes in both parents. This fly, a female, was able to live and reproduce. These two cases are not, however, equivalent since the ten-chromosome *Drosophila* had the regular female content plus two Y chromosomes which are not known to influence the production of characters except that absence of the Y chromosome causes sterility of the males.

Whether a zygote containing a duplicated pair of chromosomes can go through development may depend entirely upon which pair is duplicated. From our knowledge of the chromosome numerical variations in *Oenothera* and *Primula* certainly it is possible for a plant to develop to maturity with one extra chromosome or with an entire duplicate set.

The behavior of the seven-chromosome *Crepis* hybrid leads us to believe that there is not such a direct relationship between the two parent species as Rosenberg suggests. However, this in no way does violence to Rosenberg's hypothesis, for *C. tectorum* may behave in quite a different way when crossed with some other three paired chromosome species of *Crepis*.

It is possible that more light may soon be thrown upon this side of the problem inasmuch as there are now 36 species of *Crepis* with which trial crosses are being made to further test their chromosome relationships.

<sup>1</sup> Clausen, R. E., and Goodspeed, T. H., *Proc. Nat. Acad. Sci.*, **2**, 1916 (240-44).

<sup>2</sup> Rosenberg, O., *Arkiv. för Botanik.*, **15**, 1918 (11).

<sup>3</sup> Bridges, C. B., *Genetics*, **1**, 1916 (1-52; 107-63).